Arthropoda Selecta 10 (2): 137–146

On the identity of the European hothouse millipede *Amphitomeus attemsi* (Schubart, 1934), with first biological observations of this parthenogenetic species (Diplopoda: Polydesmida: Oniscodesmidae)

Об идентичности европейской оранжерейной диплоподы *Amphitomeus attemsi* (Schubart, 1934) с первыми наблюдениями за биологией этого вида (Diplopoda: Polydesmida: Oniscodesmidae)

Sergei I. Golovatch*, Sven Knapinski & Joachim Adis****
С. И. Головач*, С. Кнапински и Й. Адис****

* Institute for Problems of Ecology and Evolution, Russian Academy of Sciences, Leninsky pr. 33, Moscow 117071 Russia.
* Институт проблем экологии и эволюции РАН, Ленинский пр., 33, Москва 117071 Россия.
** Max-Planck-Institute for Limnology, Tropical Ecology Working Group, August-Thienemann-Str. 2, Plön 24306 Germany.
** Институт лимнологии им. Макса Планка, Рабочая группа тропической экологии, Аугуст-Тинеманн-Штрассе 2, Плён 24306 Германия.

KEY WORDS: Diplopoda, *Amphitomeus*, taxonomy, biology, gut microflora, parthenogenesis, hothouse, Europe, Neotropics.

КЛЮЧЕВЫЕ СЛОВА: Diplopoda, *Amphitomeus*, таксономия, биология, кишечная микрофлора, партеногенез, оранжерея, Европа, Неотропики.

ABSTRACT: The status of the parthenogenetic millipede *Amphitomeus attemsi* (Schubart, 1934), a common European hothouse species originally described in *Detodesmus* Cook, 1896, is revised. Discovery among several hundred females of an apparently residual (= atavistic) male each in hothouses in Berlin, Freiburg and Kiel, Germany allows confirmation of *Amphitomeus* Verhoeff, 1941 as a “good” genus based on both male genitalic structure and certain peripheral characters, largely plesiomorphic. Based on biogeographical evidence, apparently the origin centre of *A. attemsi* lies somewhere in the northwestern Andes whence it has become introduced and established in Europe and southeastern Brazil. In Europe at least, its life history seems to require at least one year and the species basically feeds on rotting wood. Experimental data on platable gut microflora and its cellulase activity show fungi and actinomycetes, but apparently not bacteria, to be highly cellulose-dependent. Lectotype selection has been made for *Oniscodesmus aurantiacus* Peters, 1864.

РЕЗЮМЕ: Ревизован статус партеногенетического многосвяза *Amphitomeus attemsi* (Schubart, 1934), обычного европейского оранжерейного вида, впервые описанного в составе рода *Detodesmus* Cook, 1896. Обнаружение среди сотен самок по одному, очевидно, остаточному (= атавистическому) самцу в оранжереях Берлина, Фрайбурга и Киля (Германия) позволило подтвердить, что на основании как строения гениталий, так и определенных внешних признаков, в основном плезиоморфных, *Amphitomeus* Verhoeff, 1941 — “хороший” род. На основе биогеографических данных, возможно, центр происхождения *A. attemsi* находится где-то в Северо-Западных Андах, откуда вид был завезен и прижился в Европе и Юго-Восточной Бразилии. По крайней мере в Европе продолжительность его развития, возможно, превышает один год, а сам вид питается на разлагающейся древесине. Экспериментальные данные по высеваемой кишечной микрофлоре и ее целлюлазной активности показывают, что грибы и актиномицеты, но, видимо, не бактерии очень сильно целлюлозозависимы. У вида *Oniscodesmus aurantiacus* Peters, 1864 обозначен лектотип.

Introduction

The original description of the oniscoid millipede *Detodesmus attemsi* Schubart, 1934 was based on several “immature” specimens taken from two hothouses in the Botanical Garden at Berlin-Dahlem, Germany [Schubart, 1934]. Following a written advice of C. Attems he cited, Schubart assigned his species to *Detodesmus* Cook, 1896, thus altering his own earlier, provisional identification of that material as *Oniscodesmus* sp. [Schubart, 1931]. Based on biogeographical evidence, this species was immediately recognized as an introduced Neotropical element apparently stemming from Venezuela or Colombia.

The reasons for placing *attemsi* in *Detodesmus* rather than in *Oniscodesmus* Gervais & Goudot, 1844 were obvious from Attems’ [1926, 1940] monographs. In addition to certain gonopod traits, *Detodesmus* species were defined as possessing a well-exposed, wide telson

readily visible from above, whereas in *Oniscodesmus* species this segment was stated to be small, club-shaped and almost entirely covered from above by the paraterga of the penultimate body segment. Strangely enough, Attems [1940] forgot to include *attemsi* in his book!

By putting emphasis on the absence both of tubercles and longitudinal striae on the metaterga as well as the presence of acutangular incisions on most of the paraterga, Verhoeff [1941], in his key to the genera of Oniscodesmidae, created among several others a new genus, *Amphitomeus*, specially to incorporate *attemsi*. Schubart [1947] seems to have been unaware of Verhoeff's [1941] publication when he again referred to this species as *Detodesmus attemsi*, this time in connection with the discovery of some females and/or juveniles in São Paulo State, Brazil. Like in Europe, both Brazilian sites mentioned, São Paulo and Rio Claro, were described as clearly anthropogenic: a hothouse at university campus and a forestry nursery.

The species remained treated in *Detodesmus* even with further records coming from hothouses in Germany [Schubart, 1957] and Poland [Brodniewicz, 1957]. Schubart [1957] reported on 47 individuals but not a single male discovered in Berlin during the 1930's. The 19-segmented specimens were still believed to be subadults. Brodniewicz [1957] found this species in one of the hothouses of Kasprzak Park (before World War 2, Wilson's Park) in Poznań and only stated it occurred abundantly under orchids, in the warmest part of the hothouse. Neither the number nor the sex of the specimens were referred to. However, the introduction was suggested to have taken place already in the 1950's, because during the war the hothouse perished while in the early 1930's no millipedes had been found in that hothouse [Moszynski & Urbanski, 1932]. Brodniewicz's [1957] record in Poland was quoted twice [Stojałowska, 1961; Staręga & Stojałowska, 1974] but, following Schubart [1934, 1957], those authors also believed that only immatures had been collected.

Enghoff [1978] summarized all available information on and was apparently the first to suggest thelytoky in this species. It has since become reported from hothouses in Copenhagen, Denmark [Enghoff, 1987: sub *Amphitomeus attemsi*], Freiburg [Bellmann, 1997: sub *Detodesmus* sp.], and Kiel, Germany [Adis et al., 2001: sub *Detodesmus attemsi*].

The present paper provides new insights into the taxonomy of *Amphitomeus attemsi* as based on the first males becoming available for study. We also provide first, provisional results of observation concerning the biology of this interesting parthenogenetic introduction.

Material and methods

Copious material of *A. attemsi*, live and/or alcohol-fixed, has been received by us from hothouses in Berlin, Kiel and Freiburg, Germany, in Basel, Switzerland and in Košice, Slovakia. Besides this, *A. attemsi* has just been found in a hothouse in Budapest, Hungary [Korsós, in litt.]. Furthermore, the population from the Tropenhaus in Kiel has been monitored for about 2 years, with several attempts undertaken to keep it in culture like we succeeded with a few other parthenogenetic hothouse Polydesmida [Adis et al., 2001; Golovatch et al., 2001a]. Three males have been discovered, one each in Freiburg, Kiel, and Berlin.

The bulk of the study material is in the collection of J. Adis at MPIL / Plön, where most of the experimental work has been conducted. A few samples, including the male from Berlin, are donated to the Zoological Museum of the Moscow State University (ZMUM), Russia. The Freiburg male is in the collection of J. Spelda in Stuttgart while the Kiel male, several females and immatures are in the Muséum d'histoire naturelle in Geneva (MHNG), Switzerland.

Numerous scanning electron micrographs (SEM) have been taken using a Zeiss Nanolab 7 microscope.

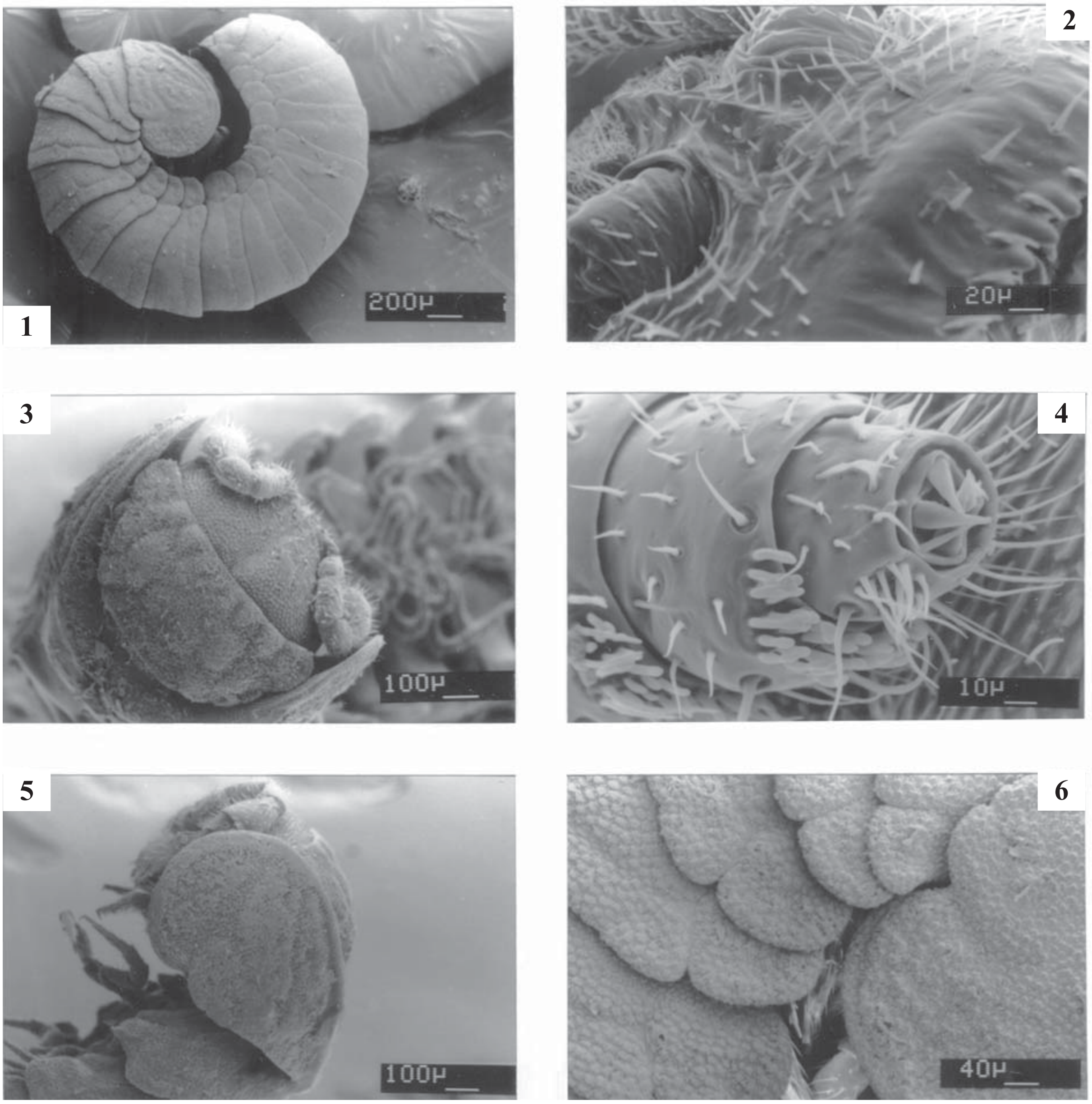
Taxonomy

Inasmuch as present-day millipede systematics is largely based on male genitalic structures, in the absence of male material any judgment about the status of about any helminthomorph millipede is bound to remain arbitrary. An additional difficulty lies in studying the parthenogenetic forms, in which males are usually from rare to non-existent. Thelytoky, i.e. a strongly female-biased sex ratio, is quite usual among exotic millipedes introduced in European hothouses, i.e. *Poratia digitata* (Porat, 1889), *P. obliterata* (Kraus, 1960), *Cylindrodesmus hirsutus* Pocock, 1889 [Adis et al., 2001; Golovatch & Sierwald, 2001; Golovatch et al. 2001a, b], and *Amphitomeus attemsi*. Acquisition of male samples in *A. attemsi* has always been a serious challenge but at the same time it remained crucial for finally solving the riddle concerning the identity of both *attemsi* and *Amphitomeus*. In addition, *attemsi* has never been described adequately, because Schubart [1934, 1957] believed he only had immature specimens at hand. In fact he did have at least one adult female, as 19, not 20, body segments is characteristic of *attemsi* adults.

Amphitomeus attemsi (Schubart, 1934)
Figs 1–28.

Oniscodesmus sp. — Schubart, 1931: 82.
Detodesmus attemsi Schubart, 1934: 168.
Amphitomeus attemsi — Verhoeff, 1941: 53; Enghoff, 1987: 148.
Detodesmus attemsi — Schubart, 1947: 30; 1957: 23; Brodniewicz, 1957: 273; Stojałowska, 1961: 115; Staręga & Stojałowska, 1974: 22; Enghoff, 1978: 79; Adis et al., 2001: 168.
Detodesmus sp. — Bellmann, 1997: 286.

Material: Germany: Kiel University Campus, Botanical Garden, Tropenhaus, in rotting wood, leg. J. Adis, B. Hansen, S. Knapinski, L. Wilck, S. Golovatch — several hundred females + several subadults + 1 male (MHNG), 23.08.2000, leg. S. Knapinski; Freiburg Botanical Garden, Tropenhaus, leg. S. Knapinski — several dozen females + 1 male (Coll. J. Spelda), 20.01.1997, leg. H. Bellmann; Berlin Botanical Garden, Tropenhaus, leg. M. Zerm — several dozen females + 1 male (ZMUM), 4.05.2000, leg. M. Zerm; Switzerland: Basel, Botanical Garden, Tropenhaus — about 20 females, leg. S. Knapinski; Slovakia: Košice, leg. A. Mock — several dozen females.

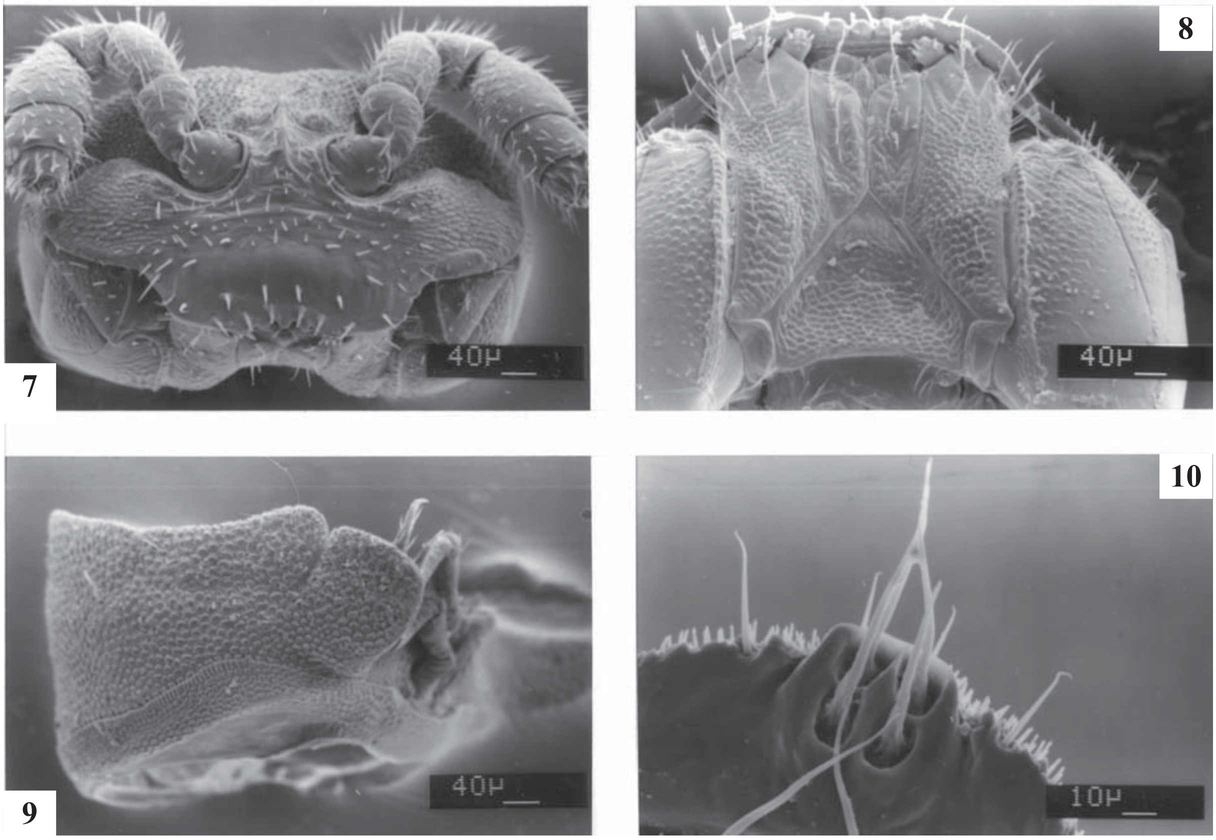


Figs 1–6. Some structural details in *Amphitomeus attemsi* (Schubart, 1934), females from Kiel: 1 — habitus, lateral view; 2 — labrum and clypeolabral region, dorsolateral view; 3, 5 & 6 — anterior body part, dorsal, lateral, and lateral views, respectively; 4 — distal antennomeres, subdorsal view. Scale bar in μm.

Рис. 1–6. Некоторые детали строения *Amphitomeus attemsi* (Schubart, 1934), самки из Киля: 1 — габитус, вид сбоку; 2 — лабрум и клипеолабральный район, вид сверху и сбоку; 3, 5 и 6 — передняя часть тела, соответственно сверху, сбоку и сбоку; 4 — дистальные членики антенн, вид примерно сверху. Масштаб в μм.

DESCRIPTION: Length of adults ca. 2.9–3.2 (male 3.0), width 0.7–0.9 mm (male 0.8). Colour often uniform pale brownish to yellow-brown, sometimes with paler fore parts of metaterga; venter, legs and antennae pallid.

Body with 19 segments (17+1+T), shape typical of Oniscodesmidae (Fig. 1), with caudal body end drastically tapered toward a relatively small but broad telson (twice broader than high) readily visible from above and not concealed by previous paraterga (Figs 17–19). Head strongly transverse (Fig. 7), not granulated, labrum rugulose, interantennal isthmus with a small but evident longitudinal ridge (Fig. 2), vertex scaly to very indistinctly tuberculate, gnathochilarium usual (Fig. 8). Antennae short, clavate, antennomere 5 larger than 6th, each with a distodorsal corolla/group of longish but thick, bacilliform sensilla, antennomere 7 with a more compact group of similar but shorter and smaller sensilla (Fig. 4). Collum inverted subtrapeziform (corners rather broadly rounded), relatively small, not covering the head from above, with highly indistinct bosses (Fig. 3). Tergum 2 particularly strongly enlarged as usual, not excavate but regularly convex toward anterior mar-



Figs 7–10. Some structural details in *Amphitomeus attemsi* (Schubart, 1934), females from Kiel: 7 & 8 — head, front and ventral views, respectively; 9 — midbody somite, lateral view; 10 — telson, ventrocaudal view. Scale bar in μm.

Рис. 7–10. Некоторые детали строения *Amphitomeus attemsi* (Schubart, 1934), самки из Киля: 7 и 8 — голова, соответственно спереди и снизу; 9 — среднетуловищный сегмент, вид сбоку; 10 — тельсон, вид снизу и сзади. Масштаб в μм.

gin, its paraterga broadly rounded, vertical, each set off caudally by a narrow suture marking a shelf-like structure where several subsequent paraterga would hinge into to conceal the lower part of paratergite 2 during volvation (Figs 1, 3, 5 & 6). Terga very strongly arched (Figs 1, 6, 11, 13, 14), rather smooth but dull due to scaly texture with micropilosity (Figs 5, 9, 11, 12, 15–19, 21), each with a barely traceable transverse suture marking a barely elevated ca. 1/3 rear, metatergal part (Fig. 1), both areation and limbus virtually absent but prozonital part and rear edge with peculiar scaly structures (Figs 15 & 16). All paraterga subsequent to 2nd (sub)vertical, set off by a narrow, deep but evident incision both anteriorly and posteriorly (Figs 6, 9, 11). Tergal setae very short, scarce, usually only preserved on few posteriormost somites mostly closer to lateral edges, normally inconspicuous against dense micropilosity (Figs 17 & 18), likely just broken off and only preserved as micropilosity. Ozopores inconspicuous, flush open on tergal surface a little below midway of caudal paratergal incision, increasingly but slightly shifted caudad toward telson (Figs 6, 19, 22), ozopore formula normal (5, 7, 9, 10, 12, 13, 15–18). Telson, like entire body but sterna, scaly and micropilose, relatively small; epiproct very short and stout, nearly fully concealed from above, surmounted with four conspicuous macrosetae in pits (Figs 10, 17–19); ventral pair of macrosetae on paraprocts more strongly apart than dorsal pair (Fig. 18); hypoproct subtrapeziform, with a paramedian pair of long, relatively poorly separated macrosetae on small knobs (Fig. 18).

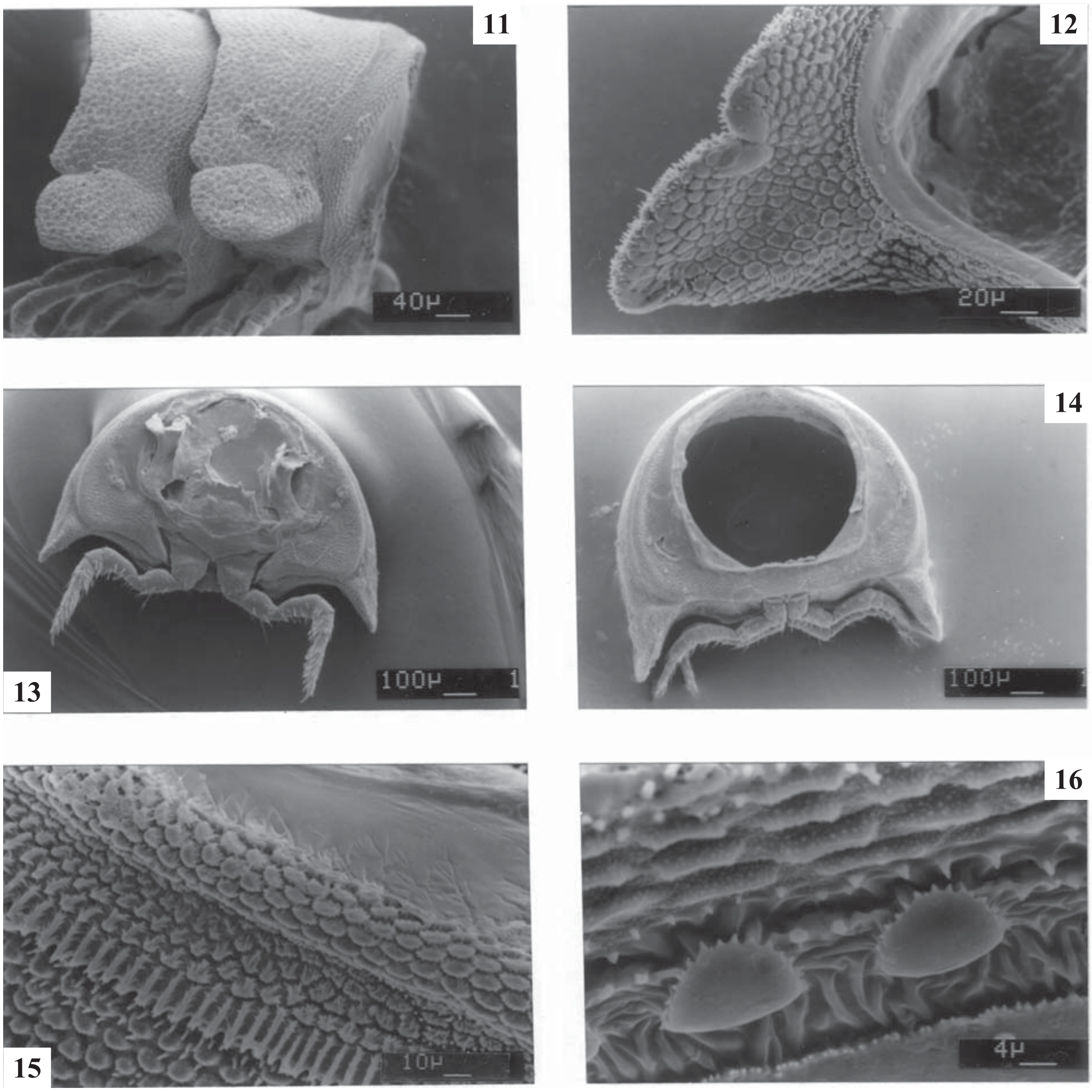
Sterna very narrow, largely with a small but evident cavity frontomedially (Fig. 20); most coxae nearly contiguous medially (Fig. 25). Legs rather short, simple, not very heavily setose, strongly flattened sagittally (Figs 13, 14, 24 & 25). Male leg coxa 2 without any marked protuberances. Epigynal ridge behind female legs 2 rather low, inconspicuous (Figs 13 & 24).

Gonopod as in Fig. 27. Coxites small, fused medially, bare, devoid of a gonocoel and of any outgrowths, laterally faintly scaly and microtuberculate, cannula somewhat foliate distally. Telopodite also small, only a little longer than coxite, suberect; prefemur swollen caudolaterad, poorly setose but apically with three disproportionately strong setae; femorite like a more distomesally shifted, hyaline lobe supporting a minor solenomerite and a fringed lobule apically, only slightly higher than prefemur.

Vulva (Figs 23 & 28) very small, like a relatively simple, stout, poorly sclerotized, quite setose sac devoid of any spiral structures inside as well as of gutter- or ridge like structures on surface. Operculum and edges of bursa with particularly strong and long setae almost reaching the end of femorite.

Discussion of the status of *Amphitomeus*

The family Oniscodesmidae as currently defined [Hoffman, 1980, 1982; Simonsen, 1990] contains 8-9

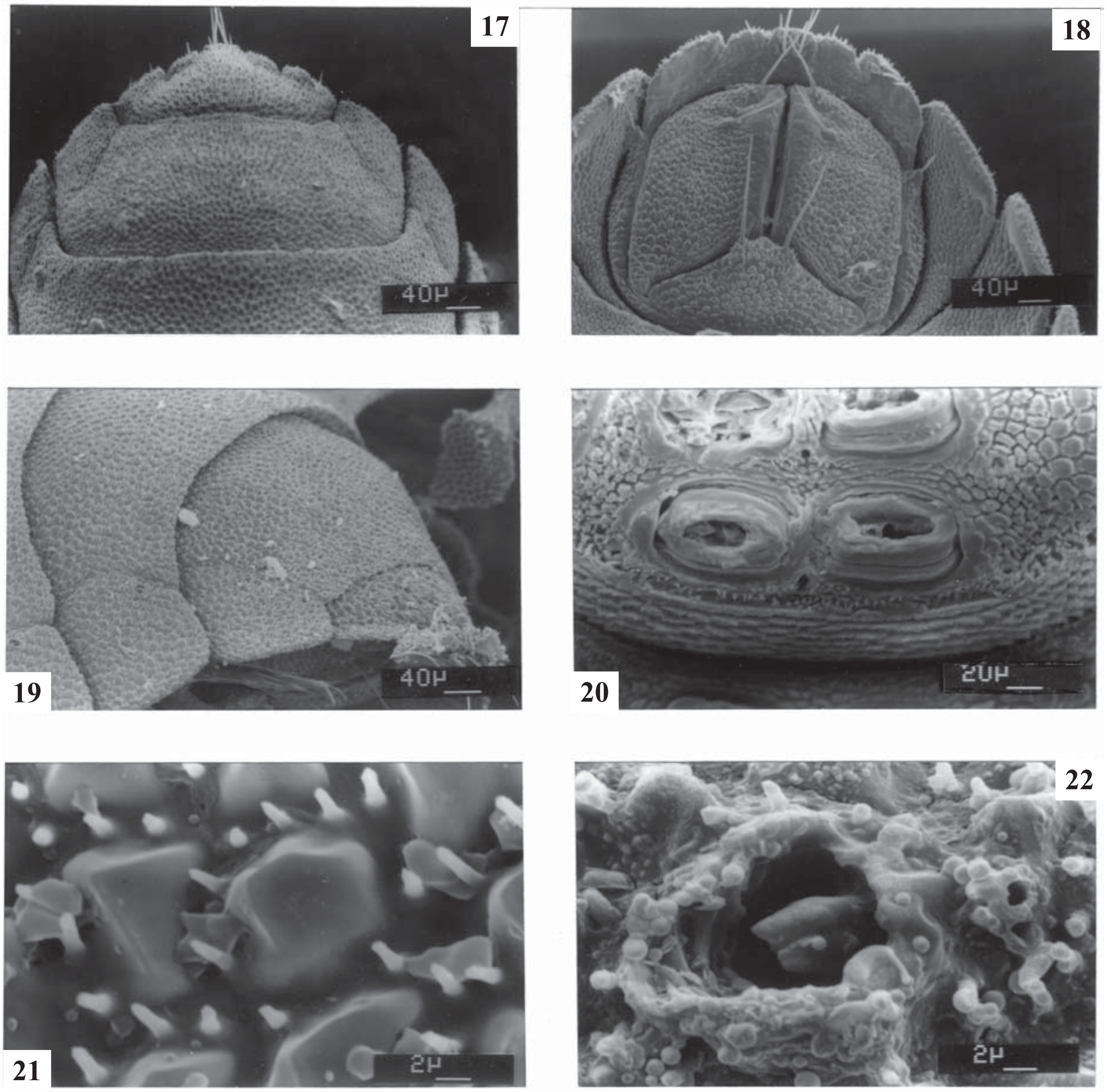


Figs 11–16. Some structural details in *Amphitomeus attemsi* (Schubart, 1934), females from Kiel: 11 — midbody somites, lateral view; 12 — left midbody paratergite, caudal view; 13 — somite 3, front view; 14 — midbody somite, caudal view; 15 — prozonital microsculpture, dorsal view; 16 — microsculpture at caudal edge of metaterga, subcaudal view. Scale bar in μm.

Рис. 11–16. Некоторые детали строения *Amphitomeus attemsi* (Schubart, 1934), самки из Киля: 11 — среднетуловищные сегменты, вид сбоку; 12 — левый среднетуловищный паратергит, вид сзади; 13 — 3-й сомит, вид спереди; 14 — среднетуловищный сегмент, вид сзади; 15 — микроскульптура прозонита, вид сверху; 16 — микроскульптура у заднего края метатергитов, вид почти сзади. Масштаб в μм.

nominal genera, all in South and/or Central America. As noted above, *Amphitomeus* has been discriminated by having paratergal incisions both anteriorly and posteriorly combined with lack of tubercles and longitudinal striae on the terga [Verhoeff, 1941]. In addition to these peripheral, often plesiomorphic traits, *Amphitomeus* can currently be characterized by the particularly simple gonopods, in which the coxite is only barely shorter than the telopodite, the latter being composed of a relatively prominent, caudolaterad shifted prefemur and a similarly short, distomesal, hyaline femorite with a short solenomerite apically.

Amphitomeus is indeed quite distinct from *Detodesmus* not only in somatic characters (19 body segments, lack of metatergal areation, a regularly convex tergite 2, a considerably smaller body size, etc.) but also in gonopod structure, which is far more elaborate in *Oniscodesmus aurantiacus* Peters, 1864, the type species of *Detodesmus* [cf. Cook, 1896]. We have borrowed both syntype male (No. 245, Venezuela, Carácas, leg. Goll-

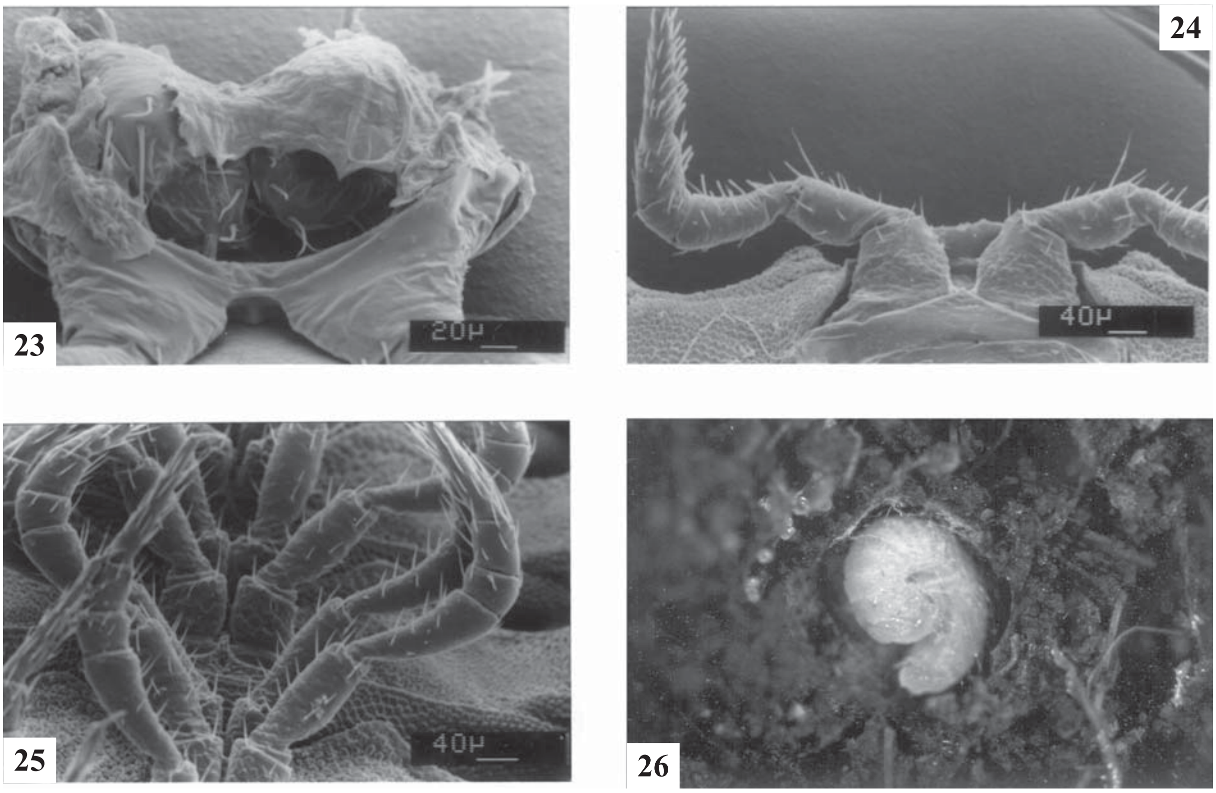


Figs 17–22. Some structural details in *Amphitomeus attemsi* (Schubart, 1934), females from Kiel: 17–19 — caudal body part, dorsal, ventral, and lateral views, respectively; 20 — sternal region of a midbody segment (legs removed), ventral view; 21 — typical scaly and micropilose microsculpture on body surfaces, dorsal view; 22 — midbody ozopore, lateral view. Scale bar in µm.

Рис. 17–22. Некоторые детали строения *Amphitomeus attemsi* (Schubart, 1934), самки из Киля: 17–19 — задняя часть тела, соответственно сверху, снизу и сбоку; 20 — стернальный район среднетуловищного сегмента (ноги удалены), вид снизу; 21 — типичная чешуйчато-микроворсистая микроскульптура поверхности тела, вид сверху; 22 — среднетуловищная пора защитной железы, вид сбоку. Масштаб в µм.

mer) and syntype female (No. 4475, Venezuela, Carácas, leg. Gollmer) of *O. aurantiacus* from the Museum für Naturkunde in Berlin, Germany (courtesy of J. Dunlop) and find the redescription and illustrations provided by Cook [1896], and repeated by Attems [1940], perfectly accurate. We take this occasion to herewith select the male as lectotype, and the female as paralectotype. The designation is the more so important as the lectotype is not only a male but it is in better condition than the fragmented paralectotype.

In other words, based now not only on peripheral characters but on gonopod structure as well, the present study provides additional support to considering *Amphitomeus* as a genus quite distinct among the known Oniscodesmidae. Regrettably, emphasizing the poor state of the art, we can only agree with Hoffman [1982: 723] that "Eight nominal genera are very provisionally referred to this family, and most require careful restudy to confirm their status". Now at least the case of *Amphitomeus* seems to be resolved. Against this background,



Figs 23–26. Some structural details in *Amphitomeus attemsi* (Schubart, 1934), females from Kiel: 23 — vulvae in situ, caudal view; 24 — epigynal region, front view; 25 — midbody legs, frontoventral view; 26 — subadult in moulting chamber. Scale bar for Figs 23–25 in µm, Fig. 26 without scale.

Рис. 23–26. Некоторые детали строения *Amphitomeus attemsi* (Schubart, 1934), самки из Киля: 23 — вульвы на месте, вид сзади; 24 — район эпигины, вид спереди; 25 — среднетуловищные ноги, вид спереди и снизу; 26 — субадультный экземпляр в линочной камере. Масштаб для рис. 23–25 в µм, рис. 26 без масштаба.

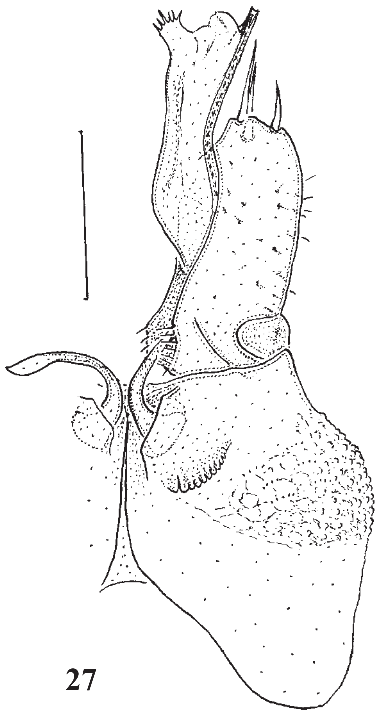
Simonsen's [1990] speculations about the evolution and biogeography of genera within Oniscodesmidae seem too premature, especially his consideration of *Crypturodesmus* Silvestri, 1897 (Brazil and Argentina) as the most basal of the genera.

To summarize, *Amphitomeus* can be diagnosed as follows:

Amphitomeus Verhoeff, 1941

Amphitomeus Verhoeff, 1941: 53.
Amphitomeus — Hoffman, 1980: 183; Simonsen, 1990: 49.
Type species: *Detodesmus attemsi* Schubart, 1934

Small-sized (ca. 3 mm long) typical Oniscodesmidae with 19 (17+1+T) body segments in both sexes. Telson readily visible from above, not covered by paraterga of penultimate somite. Ozopore formula normal. Terga generally smooth, devoid of areation but with a scaly and micropilose texture



27



28

Figs 27 & 28. Genitalia of *Amphitomeus attemsi* (Schubart, 1934), male from Freiburg (27), female from Kiel (28): 27 — left gonopod, caudal view; 28 — vulva, subcaudal view. Scale bar 0.1 mm.

Рис. 27 и 28. Гениталии *Amphitomeus attemsi* (Schubart, 1934), самец из Фрайбурга (27), самка из Киля (28): 27 — левый гоноподий, вид сзади; 28 — вульва, вид примерно сзади. Масштаб 0,1 мм.

nearly all over; paraterga set off with an anterior and a posterior incision. Gonopods very simple, coxite and telopodite of comparable length, telopodite composed of a relatively prominent, caudolaterad shifted prefemur and a similarly short, distomesal, hyaline femorite with a short solenomerite apically.

Country of origin: Unknown.

Amphitomeus currently appears to contain a single parthenogenetic species, *A. attemsi*, quite widespread over European hothouses and also reported from man-made habitats in São Paulo State, Brazil. Certainly none of these places, even Brazil, can be suggested as a plausible source area for this species. Following Schubart [1934, 1947], we are also inclined to believe that *A. attemsi* might stem from somewhere in the northwestern Andes, most likely Venezuela and/or Colombia. It would be extremely instructing to find out if thelytoky is characteristic of the *A. attemsi* populations in the source area as well, i.e. if this species is strictly parthenogenetic.

One may wonder if, given the definitely atavistic, residual, apparently non-functional (= spanandric) males in European hothouses, *A. attemsi* gonopods would be modified or at least look simpler than those deriving from conspecific but bisexual populations if any. All available evidence, however, speaks against such a suggestion. Thus, in the polydesmoid *Poratia obliterata* (Pyrgodesmidae), a 20-segmented Neotropical species whose bisexual populations occur throughout Amazonia as well as in Panama and Costa Rica while parthenogenetic populations on open terrain in Georgia, U.S.A. but only in hothouses in Europe, there are almost no differences in gonopod conformation traced between males of either bisexual or thelytokous stem. The gonopod looks a little more elaborate compared to the norm only in the 19-segmented, atavistic, spanandric males, thus somewhat approaching the condition observed in the obligatorily parthenogenetic congener *P. digitata*. The latter species is 19-segmented and its gonopods are among the most complex within *Poratia* Cook & Cook, 1894. *P. digitata* are free-living in the southern U.S.A., U.S. Virgin Islands and Java, maybe also in Panama and Costa Rica, but strictly hothouse in Europe and the northern U.S.A. [Adis et al., 2001; Golovatch & Sierwald, 2001]. Similarly, in the polydesmoid *Cylindrodesmus hirsutus* (Haplodesmidae) the gonopods from bisexual populations, all occurring in the tropics only, are barely distinguishable from those of atavistic males deriving from parthenogenetic, so-called *laniger*, populations [Schubart, 1945]. The *laniger* form occurs both in the tropics and, again in hothouses only, in Europe [Golovatch et al., 2001a, b].

Biological observations

In the hothouse of the Botanical Garden of the Kiel University, *A. attemsi* could be found everywhere but in very high densities they only occurred on heavily decomposed wood material (logs, stumps). Until very recently, cultivation of *A. attemsi* on such a diet in the laboratory failed.

The reproduction mode of *A. attemsi* seems to be annual, because first developmental stages could only be found in autumn. Adult animals occurred throughout the year, this suggesting a life span of at least one year.

Like in several other Polydesmida [cp. Adis et al., 2001], immatures build moulting chambers of soil, litter and bark material using their mouthparts. Inside a sealed chamber each juvenile produces a silken cocoon both to get protected from predators and to moult inside (Fig. 26). Four long setae at the tip of the epiproct (Fig. 10) represent a spinning apparatus [Knapinski, 2001]. The process of construction of egg chambers could not be observed. However, no silken cocoon is produced inside the egg chambers like the one known in *Poratia digitata, P. obliterata* and *Cylindrodesmus hirsutus* [Adis et al., 2001; Golovatch et al., 2001a, b].

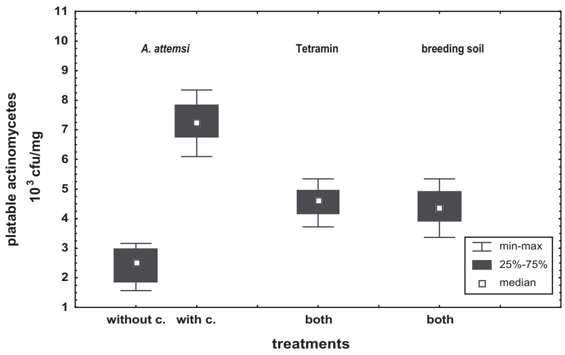


Fig. 29. Counts of platable actinomycetes in the gut of *A. attemsi* as well as in the dry fish food "Tetramin" and in the breeding soil (cfu — colony-forming units; without c. — without supplementary cellulose; with c. — with supplementary pulverized cellulose; both — same with or without supplementary cellulose). Each box plot represents data from 5 specimens, with 5 replicates each.

Рис. 29. Численность высевыемых актиномицетов в кишечнике *A. attemsi*, а также в сухом рыбьем корме "Тетрамин" и в почве-культурате (cfu — колониеобразующие единицы; without c. — без дополнительной целлюлозы; with c. — с дополнительной распыленной целлюлозой; both — то же с дополнительной целлюлозой или без нее). Каждая ячейка-диаграмма представляет собой данные по 5 экземплярам в 5 повторностях каждая.

Despite repeated attempts and several inoculum sources (Kiel, Freiburg, Basel, Berlin, and Košice), we tried but failed to breed *A. attemsi* at various temperatures under laboratory conditions at MPIL / Plön. Against a background of literally booming cultures of *Poratia digitata* and *P. obliterata*, both species fed and maintained on dry fish food ("Tetramin") plus some moist filter paper (cellulose) since early 1998, the apparent failure of *Amphitomeus attemsi* to accept the same diet seemed remarkable. This matter has been examined in further detail using gut microflora analysis.

First studies on the concentrations of platable fungi and actinomycetes in the gut of *A. attemsi* treated with supplementary pulverized cellulose showed a statistically significant difference compared to the measured concentrations of fungi or actinomycetes in the dry fish food "Tetramin" and in the breeding soil (p_{max}=0.036 and p_{max}=0.023, according to Mann-Whitney & Bonferoni, respectively) (cp. Table & Fig. 29).

In addition, the concentrations of platable actinomycetes and fungi but not that of bacteria in the gut varied significantly between treatments with or without supplementary cellulose (p=0.012 and p=0.035, according to Mann-Whitney, respectively) [Knapinski, 2001].

Table. Mean estimates of platable bacteria, fungi and actinomycetes in the gut of *A. attemsi* in treatments with or without supplementary pulverized cellulose, as well as in the dry fish food "Tetramin" and in the breeding soil[1].

Таблица. Средние оценки высевыемых бактерий, грибов и актиномицетов в кишечнике of *A. attemsi* в опытах с дополнительной распыленной целлюлозой или без нее, а также в сухом рыбьем корме "Тетрамин" и в почве-культурате[1].

	Cellulose		Tetramin	Breeding soil
	Without	With		
Bacteria 10^6 cfu/mg	1.45	1.72	1.53	1.45
Fungi 10^5 cfu/mg	1.4	2.33	1.32	1.18
Actinomycetes 10^3 cfu/mg	2.54	7.25	4.64	4.39

[1] cfu — colony-forming units

[1] cfu — колониеобразующие единицы

Cellulase activity was quantified in animals taken from the hothouse or fed supplementarily with pulverized cellulose in the laboratory. Cellulose digestion was studied in quantifying D-glucose and D-fructose with a UV-test. The concentration of glucose in the gut of A. attemsi before incubation was 1.27 µg/mg. After incubation of 12hs the glucose concentration increased to 76.13 µg/mg gut (mean of two runs). This is equivalent to a cellulase activity of 6.24 µg glucose/mg × h.

Between 40 and 70% of plant residues in the soil consist of cellulose [Rössler, 1961]. Its biodegradation due to cellulase activity is highly important in the process of mineralisation and, consequently, in the carbon cycle. Many animals produce cellulase either by themselves or by symbionts. Symbiont-dependent digestion is much more widespread than symbiont-independent one [Anderson et al., 1982; Cazemier et al., 1997; Zimmer & Topp, 1998a]. It has not been shown yet that millipedes possess a permanent microflora similar to that of termites [cp. Hopkin & Read, 1992]. However, *A. attemsi* might represent an exception and deserves further studies. Some cellulase activity has been determined but not truly quantified in millipedes [Nunez & Crawford, 1976; Kaestner, 1993]. In *A. attemsi* it was remarkably lower compared to the woodlouse *Porcellio scaber* (15–25 mmg glucose/mg x h; Zimmer & Topp [1998b]).

The mortality of *A. attemsi* in laboratory cultures could be reduced by feeding animals additionally with pulverized cellulose. Those animals kept without cellulose, dry fish food ("Tetramin") and breeding soil died after about two weeks. Thus neither gut fungi nor actinomycetes in the gut of *A. attemsi* can probably exist without cellulose. Both these microflora groups seem to be important symbionts because of their significant differences in concentration found with or without cellulose treatments and the correlated survival rate of *A. attemsi* in the laboratory. Although bacteria were the largest group of gut microbes, differences between these treatments could not be shown.

ACKNOWLEDGMENTS: We are most grateful to Andrej Mock (Košice, Slovakia), J. Spelda (Stuttgart, Germany), and M. Zerm (MPIL / Plön) for supplying us with material, to Z. Korsós (Budapest, Hungary) and H. Bellmann (Ulm, Germany) for sharing with us some unpublished information, to J. Wytwer (Warsaw, Poland) and H. Enghoff (Copenhagen, Denmark) for sending us some literature relevant to the project, to R.L. Hoffman (Martinsville, Virginia, U.S.A.) for his revision of the manuscript, to B. Albrecht and B. Hansen (MPIL / Plön) for technical assistance. J. Dunlop (Berlin, Germany) kindly provided access to certain type material under his care. The first author (SG) is greatly obliged to PD Dr. W.J. Junk, Head of the Tropical Ecology Working Group, who helps him in obtaining grants from the Max-Planck-Society for regular visits to the MPIL; the constant support rendered to SG by the Max-Planck-Society is to be genuinely acknowledged as well.

References

Adis J., Golovatch S.I., Wilck L., Hansen B. 2001. On the identities of *Muyudesmus obliteratus* Kraus, 1960 versus *Poratia digitata* (Porat, 1889), with first biological observations on parthenogenetic and bisexual populations (Diplopoda: Polydesmida: Pyrgodesmidae) // Fragm. Faun. Vol.43 (Suppl.). P.149–170 (for 2000).

Anderson J.M., Rayner A.D., Walton, D.W.H. (eds.) 1982. Invertebrate-microbial interactions. Cambridge: Cambridge Univ. Press. 341 p.

Attems C. 1926. Myriopoda // Kükenthal W., Krumbach T. (eds.), Handbuch der Zoologie. Bd.4. S.1–402.

Attems C. 1940. Myriopoda 3. Polydesmoidea III. Fam. Polydesmidae, Vanhoeffeniidae, Cryptodesmidae, Oniscodesmidae, Sphaerotrichopidae, Peridontodesmidae, Rhachidesmidae, Macellolophidae, Pandirodesmidae // Das Tierreich. Lfg.70. S.i–xxxii+1–577.

Bellmann H. 1997. Kosmos-Atlas Spinnentiere Europas. Stuttgart: Kosmos. 304 S.

Brodniewicz I. 1957. *Detodesmus attemsi* (Schubart, 1934), nowy dla Polski gatunek dwuparca (Diplopoda) // Spraw. poznan. Tow. przyjat. nauk. T.42. No.2. S.273–274.

Cazemier A.E., Op den Camp H.J.M., Hackstein H.P., Vogels G.D. 1997. Fibre digestion in Arthropoda // Compar. Biochem. & Physiol. Vol.118A. P.101–109.

Cook O.F. 1896. American oniscoid Diplopoda of the order Merocheta // Proc. U.S. Natn. Mus. Vol.21. P.451–468.

Enghoff H. 1978. Parthenogenesis and spanandry in millipedes // Abh. Verh. naturw. Ver. Hamburg, N.F. Nos 21/22. S.73–85.

Enghoff H. 1987. *Amphitomeus attemsi* (Schubart, 1934) endnu et vaksthustusindben nyt for Danmark (Diplopoda, Polydesmida, Oniscodesmidae) // Ent. Meddr. Vol.54. P.147–148.

Golovatch S.I., Sierwald P. 2001. Review of the millipede genus *Poratia* Cook & Cook, 1896 (Diplopoda: Polydesmida: Pyrgodesmidae) // Arthropoda Selecta. Vol.9 (for 2000). No.3. P.181–192.

Golovatch S.I., Gruber J., Adis J., Knapinski S., Zerm M., Hansen B. 2001a. Parthenogenetic populations of the millipede *Cylindrodesmus laniger* Schubart, 1945 to be recorded in Europe for the first time (Diplopoda: Polydesmida: Haplodesmidae) // Ibid. Vol.9 (for 2000). No.3. P.193–198.

Golovatch S.I., Hoffman, R.L., Knapinski S., Adis J. 2001b. Review of the millipede genus *Cylindrodesmus* Pocock, 1889 (Diplopoda: Polydesmida: Haplodesmidae) // Fragm. Faun. Vol.44. No.2. P.179–201.

Hoffman R.L. 1980. Classification of the Diplopoda. Mus. hist. nat. Genève. 237 p.
Hoffman R.L. 1982. Diplopoda // Parker S.P. (ed.), Synopsis and classification of living organisms. Vol.2. P.689–724.
Hopkin S.P., Read H.J. 1992. The biology of millipedes. Oxford: Oxford Univ. Press. 233 p.
Kaestner A. 1993. Wirbellose: Diplopoda // Lehrbuch der speziellen Zoologie. Jena: G. Fischer Verl. S.1112–1214.
Knapinski S. 2001. Zur Biologie, Morphologie und Parthenogenese tropischer Polydesmida aus europäischen Gewächshäusern (Diplopoda: Polydesmida: Haplodesmidae, Oniscodesmidae und Pyrgodesmidae). Diplomarbeit, Fak. Biol. Univ. Freiburg in Breisgau & Max-Planck-Inst. Limnologie in Plön. 95 S.
Moszynski. A., Urbanski J. 1932. Etude sur la faune des serres de Poznan (Pologne) // Bull. biol. France et Belgique. T.66. P.45–76.
Nunes A.L., Crawford C.S. 1976. Digestive enzymes of the desert millipede *Orthoporus ornatus* (Girard) (Diplopoda: Spirostreptidae) // Compar. Biochem. & Physiol. Vol.55A. P.141–145.
Rössler M.E. 1961. Ernährungsphysiologische Untersuchungen an Scarabaeidenlarven (*Oryctes nasicornis* L., *Melolontha melolontha* L.) // J. Insect Physiol. Vol.6. P.62–80.
Schubart O. 1931. Die Diplopoden // Das Naturschutzgebiet Schildow, Kalktuffgelände am Tegeler Fließ. S.66–83.
Schubart O. 1934. Tausendfüßler oder Myriapoda. I: Diplopoda // Tierwelt Deutschlands. Lfg.28. S.i–viii+1–318.
Schubart O. 1945. Os Proterospermophora do Distrito Federal // Arq. Mus. Nac. Rio de Janeiro. Vol.38. P.1–156.
Schubart O. 1947. O elemento "synanthropo" e estrangeiro entre os Diplopoda do Brasil // Arthropoda. Vol.1. No.1. P.23–40.
Schubart O. 1957. Die Diplopoden der Mark Brandenburg. Eine ökologische Studie // Mitt. Zool. Mus. Berlin. Bd.33. S.3–95.
Simonsen E. 1990. Phylogeny and biogeography of the millipede order Polydesmida, with special emphasis on the suborder Polydesmidea. Mus. Zool. Univ. Bergen. 114 p.
Stojałowska W. 1961. Krocionogi (Diplopoda) Polski. Warszawa: PWN. 216 s.
Staręga W., Stojałowska W. 1974. Krocionogi — Diplopoda // Katalog fauny Polski. T.14. Pt.2. 72 s.
Verhoeff K.W. 1941. Chilopoden und Diplopoden // Titschack E. (ed.), Beiträge zur Fauna Perus. Bd.1. H.2. S.5–80.
Zimmer M., Topp W. 1998a. Do woodlice (Isopoda: Oniscidea) produce endogenous cellulases? // Biol. Fertil. Soils. Vol.26. P.155–156.
Zimmer M., Topp W. 1998b. Microorganisms and cellulose digestion in the gut of the woodlouse *Porcellio scaber* // J. Chem. Ecology. Vol.24. P.1397–1408.